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Klötzli, Frank; Grootjans, Ab P.

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Restoration of Natural and Semi-Natural Wetland Systems in Central Europe: Progress and Predictability of Developments

Frank Klötzli¹
Ab P. Grootjans²

Abstract

After almost 40 years of experience in wetland restoration in Central Europe in which vegetation changes have been monitored by means of permanent plots or vegetation maps, some light can be shed on the intrinsic dynamics of such ecosystems, showing the limits of restoration and constraints in its manipulation. Sometimes such constraints in the restoration process can be identified, mostly being constraints in nutrient availability or in the water regime, but unexpected changes can also be the result of intrinsic species fluctuations or invasive species. Unexpected vegetation developments are sometimes undesired, can be very persistent and may indicate that environmental conditions are not suitable for target communities. Unexpected developments also illustrate the limits in restoration ecology. Very often the restoration process simply proceeds along successional pathways we did not anticipate. Theories about such alternative pathways can be explored using prediction models, such as cellular automata, which can handle the results of biomonitoring very efficiently. Biomonitoring during

40 years, however, has also shown that a certain amount of unpredictability has to be taken for granted, both in natural wetlands and in areas under restoration.

Key words: bog, fluctuation, permanent plots, stable states, succession.

Introduction

Our knowledge on limits and feasibility—politically and scientifically—of wetland restoration has increased considerably since the early 1970s when restoration ecology made its first appearance in North-west and Central Europe (Poschlod 1994; Wheeler & Shaw 1995; Pfadenhauer & Klötzli 1996; Bradshaw 1997; Brülisauer & Klötzli 1998a; Pfadenhauer & Grootjans 1999). In many European countries, much practical knowledge exists in the restoration of lakeshores, meandering riverbeds or small streams. The restoration of such rather dynamic systems is relatively easy and the results can be very satisfying from an ecological point of view.

In the scientific sector, much time has been spent studying the response of wetland ecosystems to restoration measures. We have learned much about the way these systems respond to perturbations and how we can counteract unwanted effects (Wheeler 1995). Because our scientific knowledge has increased, the quality of prediction models, based on best professional judgement, has also improved (Pickett & White 1985; Witte et al. 1992; Prach et al. 1999). In this respect, the situation has greatly improved since the early days of restoration ecology. Much information has become available on constraints of the restoration process: (1) the role of nutrient fluxes (Powlson 1994; Verhoeven et al. 1996; Brülisauer & Klötzli 1998b); (2) peat deterioration and loss after drainage (Blankenburg 1993; Schmidt 1995; Pfadenhauer & Grootjans 1999); (3) the role of seed banks and dispersal mechanisms (Nilsson et al. 1991; Poschlod 1995; Bakker et al. 1996b; Galatowitsch & van der Valk 1996; Bekker et al. 1997; Poschlod & Bonn 1998); and (4) the role of extrinsic disturbances (van Andel et al. 1987; Grootjans & van Diggelen 1995). This first wave of research on restoration ecology in Europe was partly accompanied by many studies on degradation of protected nature areas due to disturbances triggered by humans (van Dorp et al. 1985; Glenn-Lewin & van der Maarel 1992; Agnew et al. 1993; Fojt & Harding 1995; Klötzli 1995, 1997; van der Maarel 1996a, 1996b; Luken & Thieret 1997; Winkler & Klotz 1997; Peco et al. 1998; review in Klötzli 2001). Many of these authors had monitored vegetation changes using permanent plots and/or regular vegetation mapping. An inventory by Schmidt (1974) revealed that over 800 per-

¹Geobotanisches Institut ETH, Zürichbergstrasse 38, CH-8044 Zürich, Switzerland

²Address correspondence to Ab P. Grootjans, Laboratory of Plant Ecology, P.O. Box 14, 9750 AA, Haren, The Netherlands

manent plots were (unevenly) spread over several European countries (Bakker et al. 1996a) to monitor external noxious influences on natural areas. We may expect that this large amount of data on vegetation dynamics, originating from both repeated vegetation mapping and permanent plots, should at least shed some light on the natural fluctuations of species within plant communities. Analysis of such time series indeed showed much insight in species fluctuations under stable conditions (Watt 1971) and in conditions where succession had occurred (Roozen & Westhoff 1985; De Leeuw et al. 1990; Ellner & Turchin 1995). It was often observed that, although many species fluctuations could be explained after identification of changes in environmental conditions (van Noordwijk-Puijk et al. 1979; Olff et al. 1993), many other fluctuations were quite unforeseeable (Klötzli 2001).

After 30–40 years of experience in wetland restoration in Central Europe, it seems appropriate to look back on successes and failures and try to understand why unforeseen vegetation developments occur in many restored and even in natural wetlands. In this paper we will focus on unexpected species fluctuations in wetlands, while discussing vegetation changes observed in permanent plots in reference sites as well as partly restored sites. We will give special attention to the undesired and persisting vegetation stages, which may point to constraints in the restoration process.

Dynamics in Permanent Plots

The evaluation of long-term permanent plots provides not only more insight on their specific dynamics (Herben 1996), but unexpected peculiarities may also lead to questioning of ecological theories or formulation of new ecological concepts (Glenn-Lewin et al. 1992; van der Maarel & Sykes 1993; Grootjans et al. 1996; Klötzli 2001). Monitoring vegetation changes in permanent plots usually detects changes in the vegetation and generates hypotheses on possible causes of the observed changes. Only in exceptional cases do the plots show stable ecosystems (Sasser 1994). Figure 1, for instance, illustrates how individual species in a spring alder wood fluctuated widely during 23 years, while no clear change in species composition was observed. Generally, however, the following types of species response can be observed in permanent plots where changes in the environmental conditions have occurred (Fig. 2): (1) persistent or constant species that do not appear to react to changes in the environment (example: *Peucedanum palustre* [milk parsley]); (2) fluctuating without a clear trend (*Holcus mollis* [creeping soft-grass]); (3) increasing (*Poa trivialis* [meadow grass]); (4) decreasing (*Sphagnum recurvum*); and (5) intermittent (“undecided”) appearance (*Dryopteris cristata* [fern species]).

The study of long-term permanent plots has made it particularly clear that the vegetation development in many ecosystems under restoration was very different from the final state that was anticipated (Berendse et al. 1992; Beltman et al. 1995; Klötzli 1997). Quite often the plots showed developments with clear shifts to undesired and long-lasting stable states.

Unexpected Vegetation Changes During Restoration

Unexpected vegetation changes may be due to unforeseen causes, which afterwards may or may not be explained when all information is available. A properly monitored restoration project sometimes offers additional information on constraints (water, nutrients, pH) that may have caused this unexpected development (Roelofs et al. 1996), but in other cases constraints for successful regeneration could only partly be identified (van Duren et al. 1998). Monitoring the results of hydrological amelioration of the river Reuss (Switzerland) showed clear signs of rewetting in an old riverbed which contained remnants of litter meadows with the endangered *Iris sibirica* (Klötzli & Zielinska 1995; Klötzli 1997). The plots covered a time span of almost 40 years and several plots showed a sudden increase in tall nitrophilous herbs and sedges in later years, which started to fluctuate without a clear trend, particularly at the borders between vegetation types. A detailed analysis of vegetation maps revealed that shifts in vegetation types were most evident at the lower end of the height gradient. The observed changes could be related to nearby agricultural activities and to the amount of precipitation influencing the fluctuations of water levels. This example shows that we underestimated the effects of the hydrological reconstruction in the river Reuss and the role of eutrophication from agricultural use in adjoining areas (Schot & van der Wal 1992). At present the nutrient flow from agricultural areas is well under control, and the vegetation appears to be in a more or less stable state, i.e., fluctuating around a moderately eutrophicated vegetation type. This example also shows that it is very difficult to restore plant communities that we have known from the past, because environmental conditions may change in an unforeseen way.

Biological interactions may also change in an unforeseen way. Sudden changes in performance of dominant species can be caused by the occurrence of pathogenic reactions within plant communities, as was reported from dry coastal dunes, where *Hippophae rhamnoides* (sea-buckthorn) and *Ammophila arenaria* (marram grass) were attacked by soil nematodes during certain stages in the succession (Zoon 1986; van der Putten 1989). Similar fluctuations in species performance have been registered in savannah areas (Klötzli et al. 1995) within a period of 12–14 years. Several species that were very

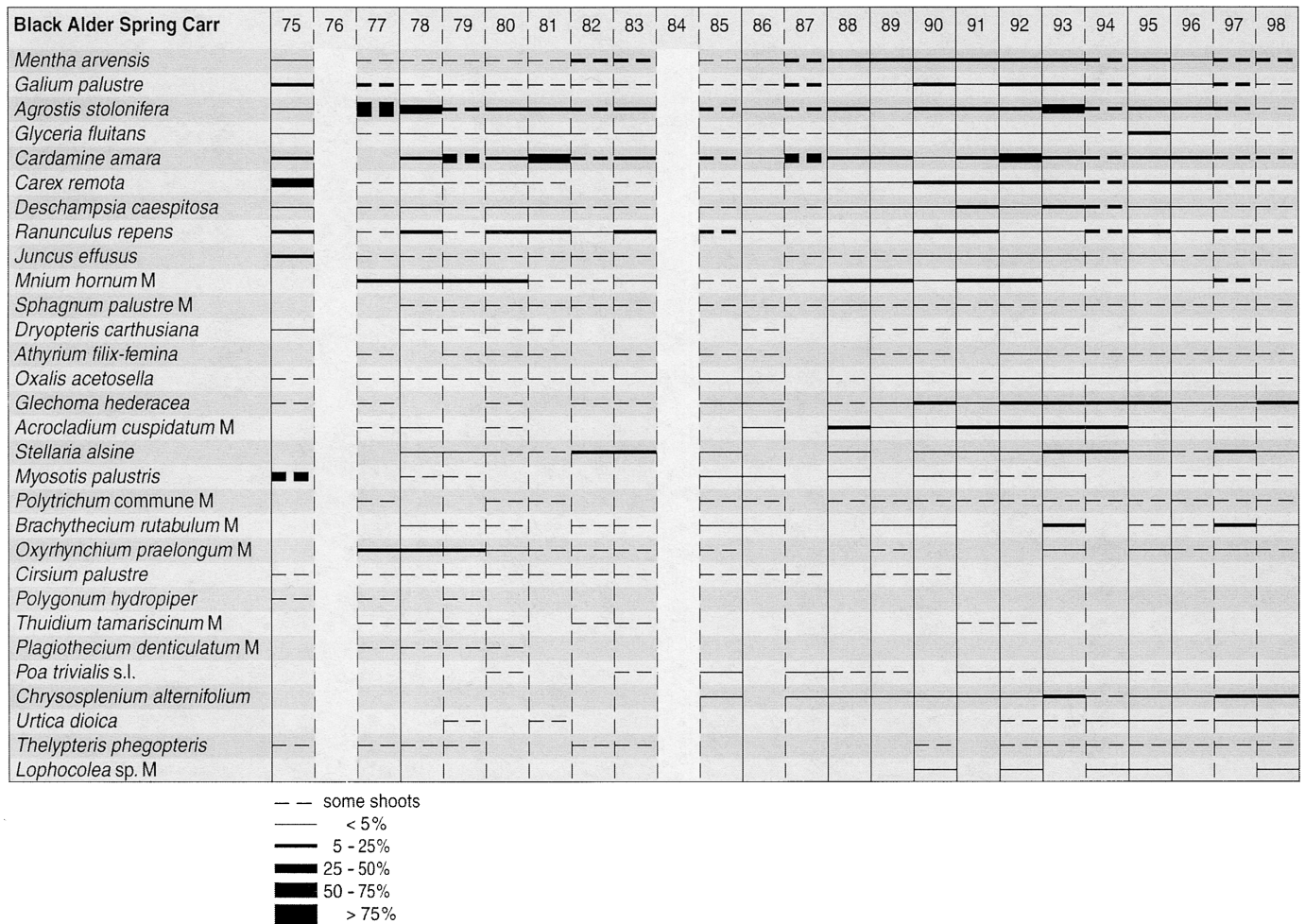


Figure 1. Vegetation dynamics in an Alder Spring Carr (*Alnus glutinosa*) at the northeastern part of the Lüneburger Heide in northern Germany (Ahrberg near Garlstorf am Walde). The species composition is fluctuating with no successional trend. M = moss species.

common between 1974 and 1980 were restricted to specific vegetation types in 1992. Common species became rare, while rare species became common. These rather abrupt changes could not be related to wet or dry years or other changes in environmental conditions (such as drought, fire or grazing) that can be responsible for mosaic vegetation patterns in savannah ecosystems (Jeltsch et al. 1998). The authors suggested that the apparent changes in site preferences of species might be connected with pathogenic reactions.

Other unexpected changes in permanent plots are caused by invaders from other continents that have established in the restoration site. Ample literature exists on this phenomenon (Drake et al. 1989; Berling 1995; Pysek et al. 1995; Klötzli et al. 1996; Luken & Thieret 1997; Starfinger et al. 1998). Well-known examples are herbs such as *Solidago canadensis*, *S. gigantea* (golden rod species), *Reynoutria japonica* (Sukopp & Sukopp 1988; Pysek et al. 1995) and shrubs, such as *Cornus stolonifera*

(red-osier dogwood) and *Prunus serotina* (wild black cherry) (Sukopp & Trepl 1987). However, "invasive behavior" in restored wetlands is not restricted to alien species, but is observed in native species as well. Examples of invasive behavior after restoration are described by Beltman et al. (1995) where *Sphagnum* species started to dominate the vegetation after sod cutting aimed at restoring basiphilous wetland communities. Klötzli (1987) reported on one of the first large-scale transplantation experiments in Europe, where mesotrophic fen and fen meadow vegetation was transplanted to an artificially constructed wetland to make room for an airport near Zürich. He found that many native species, which were present in small numbers in the original sward (*Carex hirta* [hairy sedge], *Eupatorium cannabinum* [hemp agrimony] and several *Juncus* [rush] species) expanded rapidly after some time. After much fluctuation, they finally reached a state of relative stability. This example shows that transplanted swards may reach stable states, al-

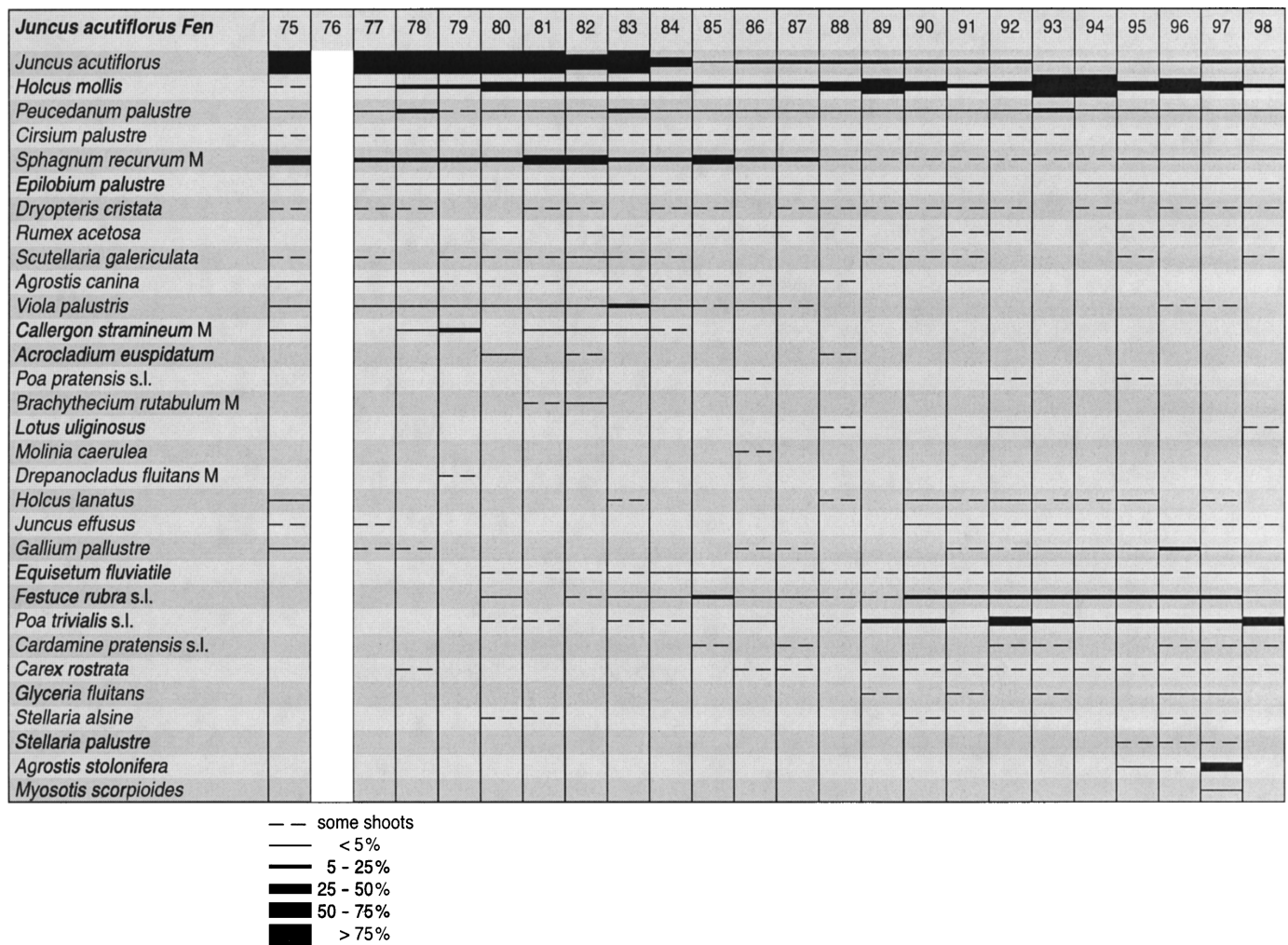


Figure 2. Vegetation changes in a *Juncus acutiflorus*-poor fen situated in the northern part of the Lüneburger Heide (near Undeloh, Germany). The vegetation changes indicate a clear successional trend toward more eutrophic wet meadows. The fen vegetation is changing due to the influences of a nearby brook, which is changing its course.

though their species composition differs from natural swards, even after 20–30 years. Such invasions or rapid expansion of dominating species can be decisive for further development of the ecosystem. A single species may initiate a vegetation stage that inhibits the development of the target community, which was anticipated at the start of the project. Such “arrested succession” (Niering & Goodwin 1974) may last for decades (van der Valk 1981, 1992).

The invasion of *Phragmites australis* (common reed) in protected fen meadows with many endangered (Red List) species is another example of this phenomenon (Güsewell & Klötzli 1998). Each stem of *Phragmites australis* was connected with nutrient pools and fluxes elsewhere in the stand (Haslam 1971). The abundance of *Phragmites* in some areas was clearly related to increased levels of soil nitrogen and phosphates (Brülsauer & Klötzli 1998b). Terrestrial stands of *Phragmites*

showed high levels of nitrogen near lakeshores or cultivated fields, suggesting perhaps that expansion of reed may be triggered by eutrophication in nearby ecosystems (Haslam 1971; Luken & Thieret 1997). Güsewell and Klötzli (1998), however, found that the loss of endangered fen meadow species was greater in fields with a combined invasion of tall herbs and *Phragmites*, compared to fields where either tall herbs or *Phragmites* had spread alone. In fact, many fields showed no significant correlation between aboveground biomass of *Phragmites* and occurrence of Red List species. The authors suggested that *Phragmites australis* could perhaps trigger a positive feedback mechanism to increase the nutrient availability in the topsoil. This deep-rooting species could transport nutrients from deeper layers to the shoots, making nutrients available for fast-growing sedges and tall herbs when *Phragmites* litter decomposed. Further experiments should solve this problem,

but the observations show that interactions may exist between different invasive species, which makes predictions on future developments difficult.

Semi-Stable States: Obstacles for Regeneration?

Restoration attempts in shallow aquatic ecosystems, such as lakes and ponds, showed that unforeseen and undesired semi-stable states could develop after restoration measures were carried out. Such stable states are the result of positive feedback mechanisms that stabilize a certain development stage (Holling 1973; Scheffer 1998). This phenomenon differs from the successional process of facilitation (Connell & Slatyer 1977), in which plants make the environment suitable for their successors. A positive feedback switch occurs when a certain vegetation state modifies its environment in such a way that it becomes more favorable for itself. In terrestrial ecosystems this phenomenon is well known (Odum 1971; Wilson & Agnew 1992; Agnew et al. 1993; van de Koppel et al. 1997). Wilson and Agnew (1992) discussed numerous switches in terrestrial ecosystems leading to vegetation states that can persist for a very long time. Switches can produce and maintain abrupt boundaries between plant communities where no obvious differences in substrate characteristics exist. In restoration projects very persistent semi-stable states are often considered as obstacles, because the goal usually is a full regeneration of a former reference state (Klötzli 1991; Wheeler & Shaw 1995; Bradshaw 1997). The occurrence of such long-lasting, but not final, states during restoration is not always clearly understood (Hobbs & Norton 1996). Certain dominating (partly invasive) plant species may last for decades (Olf & Bakker 1998), unless further perturbations change the site conditions temporarily or permanently. A bog restoration project in the Schierhorner Moor in northern Germany is a good example of the occurrence of such long-lasting intermediate stages. After raising the water table in an old pasture with *Alopecurus geniculatus* (marsh foxtail; gramineae) in 1985, *Juncus effusus* (soft rush) became the dominant species and *Carex rostrata* (beaked sedge), *C. canescens* (gray sedge) and *Agrostis stolonifera* (creeping bent) were very abundant (Fig. 3). *Sphagnum* species and *Polytrichum commune* reached the restoration area within three years and spread over approximately 1 ha, even beginning to form hummocks. Then the succession toward bog vegetation stopped. A stable state with small sedges and *Sphagnum* mats under the shade of tall *J. effusus* persisted for many decades. Possibly *J. effusus* has a similar strategy to dominate the vegetation as tussock species, such as *Molinia caerulea* (purple moor-grass) and *Eriophorum vaginatum* (cotton grass) that can coexist with *Sphagnum* swards for long periods of time. Both species

are able to reallocate nutrients very efficiently within the tussock, thus monopolizing nutrients, while successfully competing for light at the same time. Kooijman and Kanne (1993) reported on the occurrence of semi-stable states in a fen restoration project. They showed that *Sphagnum fallax* and *P. commune* rapidly expanded in pioneer stages of eutrophic terrestrializing fens and formed a vegetation stage, which was stable for at least 10 years. Whether positive feedback mechanisms are indeed operative in these examples, or environmental conditions are simply unsuitable for typical bog species, only can be discovered after carrying out proper experiments. We must realize, however, that such semi-stable states in a restoration project may sometimes function as a necessary stage toward a final target stage. The unexpected stage may function as a mechanism to reduce easily available nutrients in the soil and store them in living or dead plant tissue. Jasnowski and Kowalski (1978) reported on the establishment of *Sphagnum* hummocks on top of a shallow layer of *Cladium mariscus* (great fen-sedge) peat (53 cm). The peat had been formed in depressions in exposed lake chalk in the 100 years following an artificial drop in the lake level of Lake Tchórzyno in western Poland. The authors calculated that *Cladium* must have accumulated 20 tons of dry matter per hectare per year, which is very high. After having monopolized practically all available nutrients, some *Cladium* stands were recently invaded by *Sphagnum fimbriatum*, which formed a shallow acidic peat layer (10 cm) on top of dead remains of *Cladium*, leaving few *Cladium* shoots alive.



Figure 3. Persistent vegetation phase with dominance of *Juncus effusus* after rewetting a former agricultural grassland. Target species, such as *Sphagnum recurvum* and *Polytrichum commune*, are present in the vegetation, but are overgrown by *Juncus* tussocks.

Unsuccessful Bog Restoration: Hysteresis or Inadequate Rebuilding

In many areas of Central Europe, bogs have been nearly eliminated during the last centuries, especially during and after the Second World War. Therefore, at least the restoration of bogs is highly sponsored in some countries of the over-cultivated areas of Central and Western Europe (Vermeer & Joosten 1992; Wheeler & Shaw 1995; Pfadenhauer & Klötzli 1996; Pfadenhauer & Grootjans 1999). The restoration of large cut-over bogs, however, is not an easy task and few success stories have been reported. In some extreme cases regeneration appeared to be restricted by the mere absence of suitable peat moss species (Poschlo 1994; Rochefort et al. 1995; Grosvernier et al. 1997). In most areas with bog remnants, the species are still present but growth of typical bog species, such as *Sphagnum* spp., is stagnating, even after excessive rewetting. Results of many restoration studies (Poschlo 1995; Wheeler & Shaw 1995; Grosvernier et al. 1997) demonstrate the great number of problems in maintaining appropriate water levels, manipulating nutrient fluxes and initiating bog formation. Some authors blame increased atmospheric deposition of nitrogen and sulfur for the failure of *Sphagnum* to successfully compete with phanerogams, such as *Molinia caerulea* or

Eriophorum vaginatum (Bobbink et al. 1998). However, in small acid fens spontaneous bog formation still takes place within the same areas (northern Germany and the Netherlands). By chance we have witnessed such a "birth of a raised bog" while monitoring vegetation changes in wet heathlands in northern Germany (Lüneburger Heide). The plots were installed by Professor K. Meisel in 1975. It was anticipated that water levels and fluctuations in this part of the Lüneburger Heide would change after increased groundwater abstraction from deep aquifers which was planned to produce more drinking water for the city of Hamburg. We could not detect clear signs of dryer conditions, but instead we monitored a process of initial bog development (Klötzli 1999). This is illustrated in Figures 4 and 5, showing the first establishment of typical bog species in wet heathland sites. One by one, the peat moss species such as *Sphagnum magellanicum* and *S. acutifolium* and also *Andromeda polifolia* (bog rosemary, ericaceae; Fig. 5) appeared, after *S. recurvum* mats had been formed. Gradually, small hummocks spread on the mire surface and initiated, at least physiognomically, this first stage of a bog (Fig. 6). So, *Sphagnum* growth as such is not a problem. Lütt (1992) and Lütke Tvenhöfen (1992) clearly showed that several *Sphagnum* species grew rapidly in

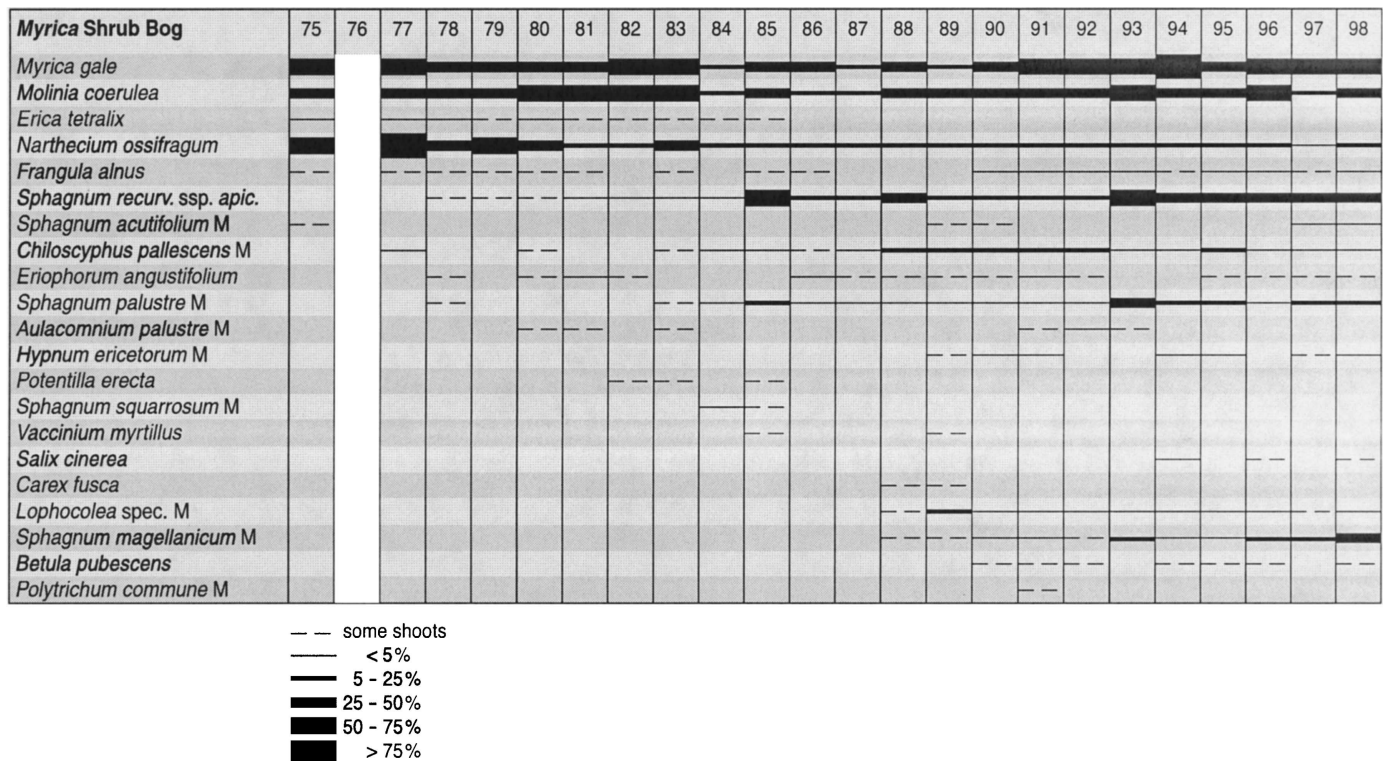


Figure 4. Vegetation development in a wet minerotrophic bog dominated by *Myrica gale* (bog myrtle) shrub. This permanent plot shows the decline of *Narthecium ossifragum* (bog asphodel) and the development of a vegetation dominated by *Sphagnum recurvum*, *S. palustre* and the typical bog species *S. magellanicum*.

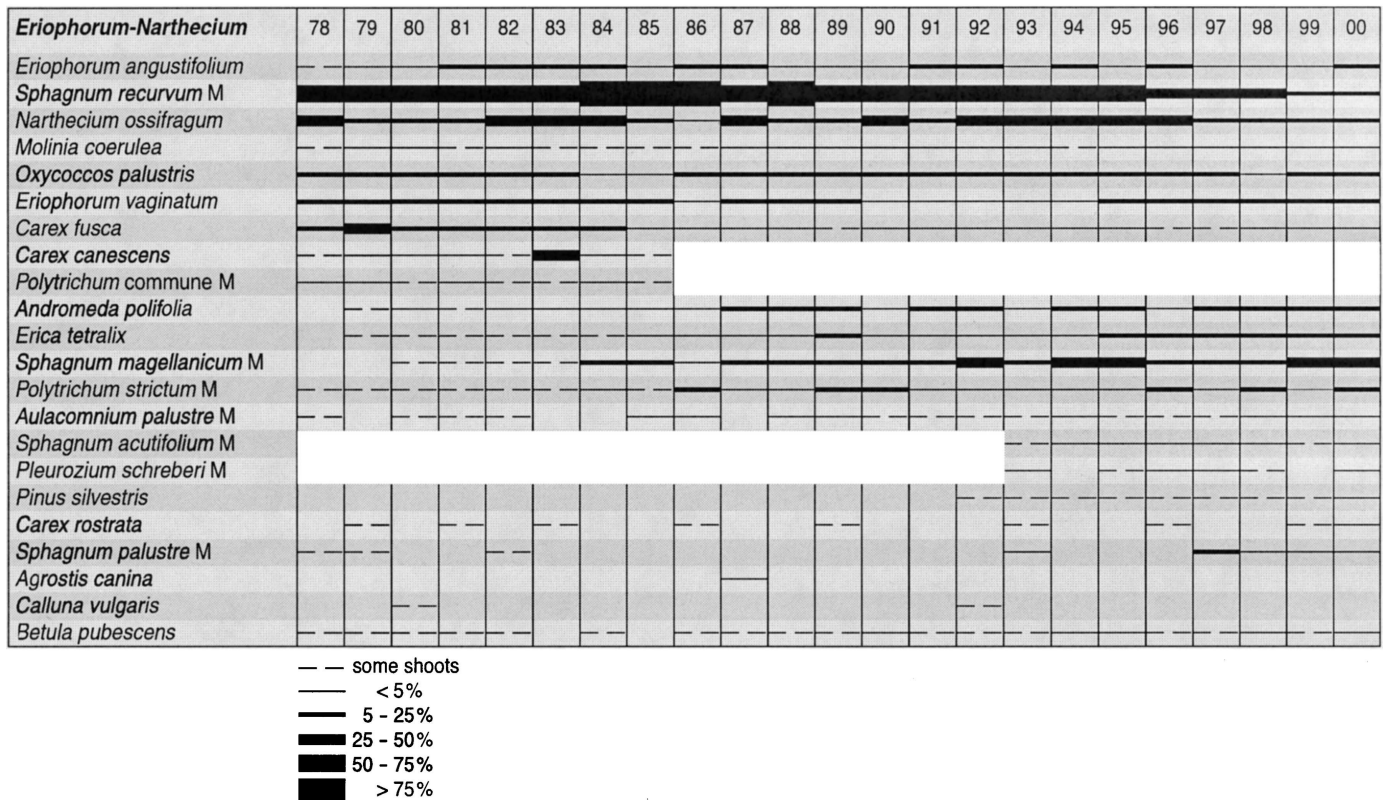


Figure 5. Vegetation development in a wet minerotrophic bog surface dominated by *Eriophorum vaginatum*, *Sphagnum recurvum* and *Narthecium ossifragum*. This bog is surrounded by wet heathlands, alder swamp forest and *Myrica gale* shrub and situated close to the Radebach, which is a small brook in the central part of the Lüneburger Heide (near Undeloh, Germany). The permanent plot clearly shows the development of *Sphagnum magellanicum* mats with *S. palustre*, and the establishment of *S. acutifolium* and *Pleurozium schreberi* (on tussocks and hummocks).

peat cuttings and were stimulated by atmospheric nitrogen deposition.

Why then is the restoration of larger bog remnants so difficult? There can be many different reasons for this, depending on different local conditions, but they all have in common that most large bog remnants have become rather unsuitable sites to restart *Sphagnum* growth. When we compare the successful process of bog formation in wet heathlands and terrestrializing fens (van Wirdum 1993; van Diggelen et al. 1996) with the clearly different process of regeneration in large bog remnants, we seem to be dealing with "hysteresis." Hysteresis is a process in which a system evolves to another state after disturbance, but when the disturbance (stressor) is removed, the system does not immediately return to its original level; instead, it takes a different and long-lasting route before it returns to its original state. It may be questioned whether in complex terrestrial ecosystems any system can return to its original state (Tallis 1991), but if hysteresis does occur in bog restoration, rewetting alone is insufficient, since the functioning of the bog as a system is inadequate. Without restoring the living top-

soil (called acrotelm), consisting of living species of *Sphagnum* and hardly-decomposed plants, bog growth is impeded. Under such conditions repairing the bog is no longer possible; it should be rebuilt (Wheeler & Shaw 1995). Solutions to this problem are numerous (Vermeer & Joosten 1992; Wheeler & Shaw 1995), but one solution is particularly effective and simple. If hydrological conditions have become suitable for *Sphagnum* growth, a mat of phanerogams, such as *Carex* or *Eriophorum* species, can be artificially installed on the rewetted bog remnant (Buttler et al. 1998). Its growth may even be stimulated by fertilization. After establishing such an artificial fen vegetation, several *Sphagnum* species, which prefer growing on mineral soils, can also form extensive mats on bog remnants under restoration and use the tall fen species (*Eriophorum vaginatum*) for support (Lütt 1992; Pfadenhauer & Klötzli 1996). In the study by Buttler et al. (1998), an "invasive" species appeared to be an essential trigger for later stages. This was also suggested by Hughes (2000), who found remnants of *E. vaginatum* and *Calluna vulgaris* peat at the interface between fen and bog peat. *Sphagnum* growth was preceded by a distinct fall in



Figure 6. General view of the minerotrophic bog (see Fig. 5) in the Lüneburger Heide showing hummock formation of *Sphagnum magellanicum* and *Polytrichum strictum* on former *Eriophorum vaginatum* tussocks and *Erica tetralix* shrubs.

the groundwater table, which must have separated the growing surface from the groundwater supply, leading to a rapid spread of *Eriophorum* tussocks. In his view, the establishment of *E. vaginatum* could well be one possible way to restore acrotelm functioning. *Eriophorum* litter is slow to decompose and contains tough leaf and rhizome fibers, producing a peat with good water retention characteristics. These examples show that certain unexpected and undesired vegetation states can have a positive contribution toward a desired and expected reference state. The succession toward such an expected reference state is very difficult to predict using only monitoring data that have been gathered during the time of degradation or during restoration. Such information can yield much insight about ecological tolerance of *Sphagnum* species, but provides little information on the conditions triggering rapid growth of bog species.

New Tools to Predict Wetland Development

Our ability to predict vegetation changes in wetlands is mainly based on experience abstracted from permanent plots and from repeated vegetation surveys, carried out to assess prominent changes in areas under restoration. Monitoring environmental conditions on a regular basis, combined with vegetation descriptions in permanent plots, has provided much insight into the regeneration prospects of damaged ecosystems. Monitoring offers opportunities to detect how species establish populations and how they disappear. Descriptive research does not provide information on mechanisms behind these phenomena; however, it generates hypotheses on possible causes for unexpected vegetation change (Ellner & Turchin 1995; Herben 1996). Both the

accumulated data and the new ideas derived from these observations can be used in prediction models, such as expert systems (Prach et al. 1999) and cellular automata (Herben 1992; Silvertown et al. 1992; Wolfram 1994; Belde & Richter 1997; Balzter et al. 1998). Cellular automata (CA), in particular, appear to be good instruments to further explore theory on vegetation succession. CA models can, for instance, predict the development of an herb layer for the next 50–100 years when fed with appropriate field data and ideas about relevant processes. Data obtained from permanent plots that have been monitored for 10–30 years appear to be very useful for CA analyses (Gassmann et al. 2000).

Conclusions

Often the final goal of a restoration project is a full and quick regeneration toward an original reference state. Often we encounter numerous unexpected changes in the vegetation, of which some can be explained afterwards when analyzing all available data gathered during the restoration process. Although much progress has been made in the fields of intrinsic vegetation dynamics, nutrient demands and fluxes, peat deterioration, dispersal mechanism and seed banks, the failure to predict deviations from regular vegetation developments during the process of ecosystem restoration illustrates some of the limits in restoration ecology.

Prediction models may help further explore theories on vegetation succession. It is very stimulating to see what the consequences of new ideas could be for the restoration process 50–100 years from now. At the same time we must realize that we have little knowledge on why and how long-lasting semi-stable states occur during restoration and how they can be influenced to change in a desired direction. Such gaps in knowledge can partly be filled by further experimentation, but we may also anticipate further unexpected fluctuations in the field during restoration, and we may move to studying the insufficiently-explored field of pathogenic cycles within plant communities.

After 40 years of monitoring, much progress has been made in understanding bottlenecks in restoration projects, but often nature does not seem to listen to our explanations. We often find ourselves in a position where we are puzzled by changing vegetation mosaics in the field and records of our permanent plots are like sheets of an illustrated calendar. We tear off the sheet, wondering what the next day will bring.

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